

Niches in two and Three dimensions.

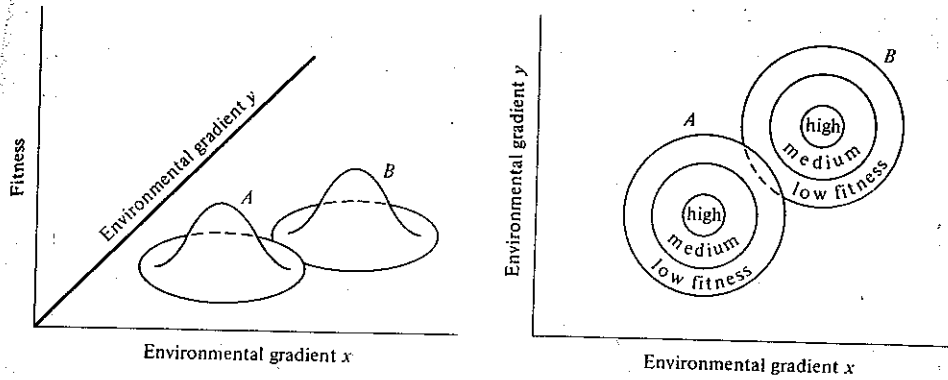


Figure 13.2 Two plots of the fitnesses of two organismic units, A and B, versus their position along two environmental gradients, x and y . (a) A three-dimensional plot with a fitness axis. (b) A two-dimensional plot with the fitness axis omitted; low, medium, and high fitness represented by contour lines.

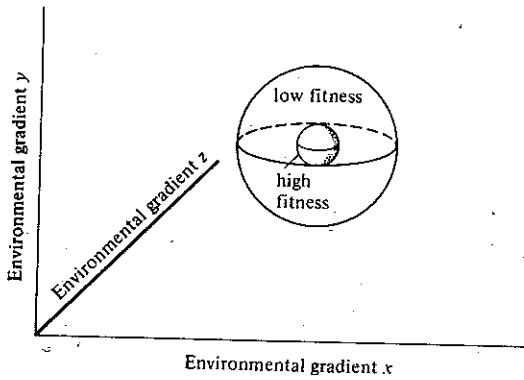
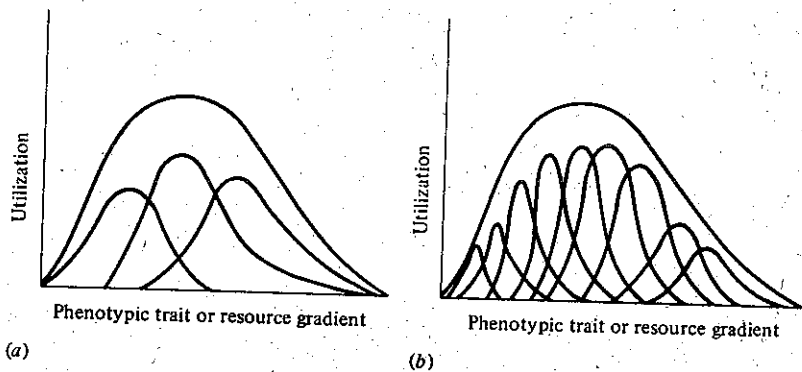


Figure 13.3 A plot (like that of Figure 13.2b) of fitness along three different environmental gradients, x , y and z , showing zones of low and high fitness. A four-dimensional plot with a fitness axis analogous to Figure 13.1a is implicit in this graph.

>3 niche axes → "Hypervolume"

Niche Breadth

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↑
Large within-phenotype
contribution to niche
breadth

↑
Large between
phenotype
contribution to
niche breadth.

Figure 13.4. Various possible niche relationships, with fitness density models on the left and set theoretic ones on the right. (a) An included niche. The niche of Species 2 is entirely contained within the niche of Species 1. Two possible outcomes of competition are possible: (1) if Species 2 is superior (dashed curve), it persists and Species 1 reduces its utilization of the shared resources; (2) if Species 1 is superior (solid curves), Species 2 is excluded and Species 1 uses the entire resource gradient. (b) Overlapping niches of equal breadth. Competition is equal and opposite. (c) Overlapping niches of unequal breadth. Competition is not equal and opposite because Species 2 shares more of its niche space than Species 1 does. (d) Abutting niches. No direct competition is possible, but such a niche relationship can arise from competition in the past and be indicative of the avoidance of competition, as in interference competition. (e) Disjunct niches. Competition cannot occur and is not even implicit in this case.

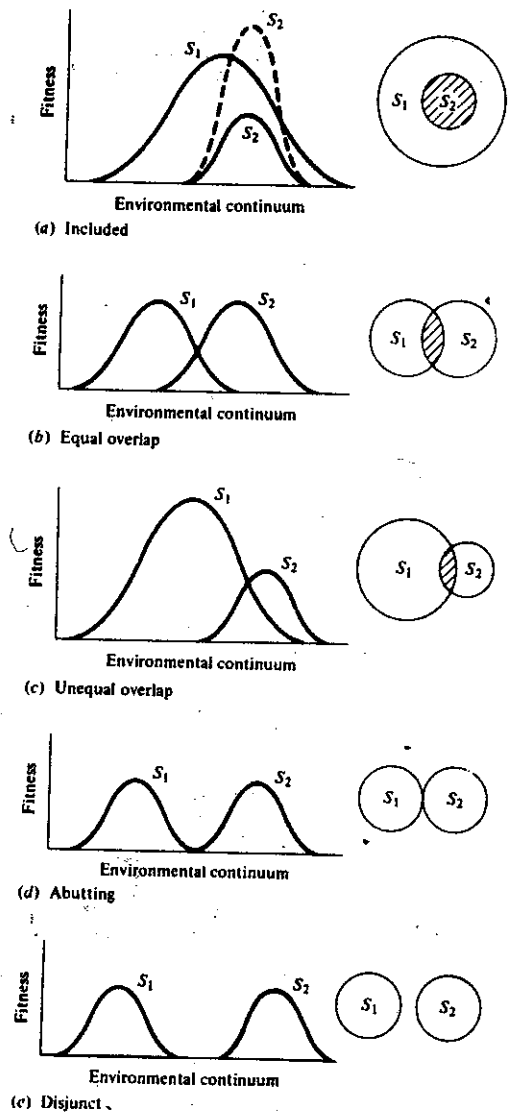
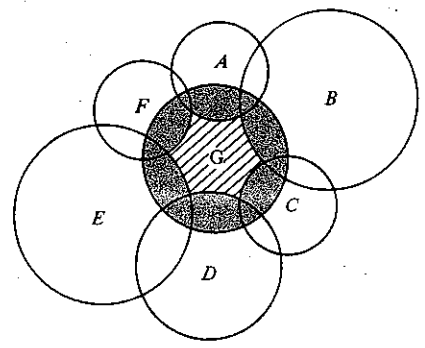
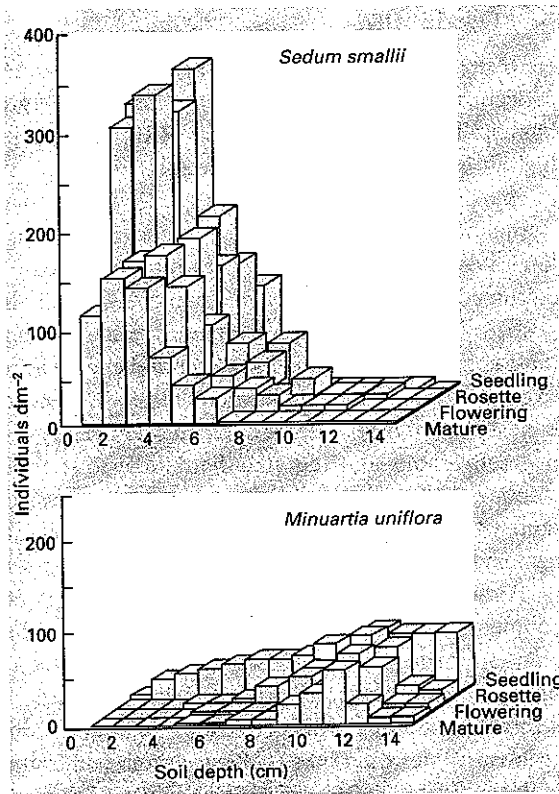


Figure 13.5. Set theory model of the fundamental niche (stippled and cross hatched) of Species G and its realized niche (cross hatched), which is a subset of the fundamental niche, after competition and complete competitive displacement due to six superior competitors, species A, B, C, D, E, and F.



Niche shifts by individuals through
 time : indeterminate growth (plants, many
 poikilotherms)
 : metamorphosis (inverts).



Little shift
 in niche

Larger shift
 in niche

Figure 7.26 The zonation of individuals, according to soil depth, of two annual plants, *Sedum smallii* and *Minuartia uniflora* at four stages of the life cycle. (After Sharitz & McCormick, 1973.)

Soil depth used by 4 stages of
 life cycle in two spp. of plants.

it is possible to find in a single tapeworm a complete developmental series of proglottids from infancy to old age. The young undifferentiated segments just behind the neck gradually attain sexual maturity in the middle portions of the worm, and then the segments either continue to produce and shed eggs throughout the rest of the strobila (in Pseudophyllidea) or there follows a gradual decadence of the reproductive glands (in Cyclophyllidea) as the segments "go to seed" and become filled by the pregnant uterus with its hordes of eggs (Fig. 86). The whole process can be likened to the development of an undifferentiated bud into a perfect flower and then a seed pod.

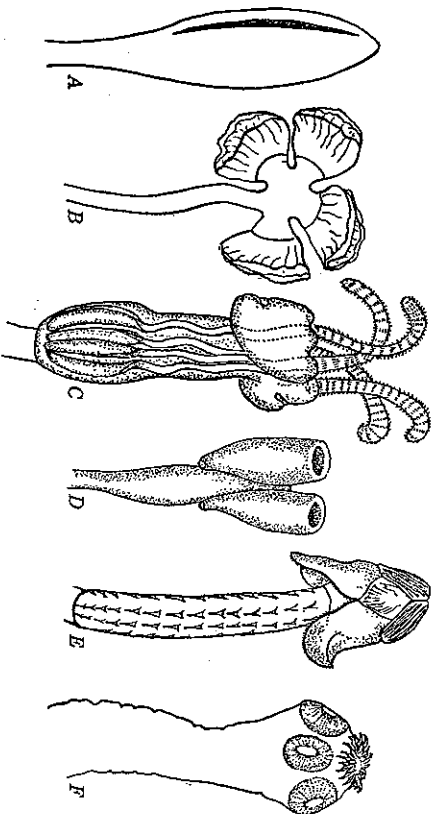


Fig. 87. Types of scoleces of tapeworms. A, order Pseudophyllidea (*Dibothriocephalus latius*); B, order Tetraphyllidea (*Phyllobothrium* sp.); C, order Trypanorhyncha (*Orobolthium* sp.); D, order Pseudophyllidea (*Bothriidium* sp.); E, order Diphyllidea (*Echinobolthium* sp.); F, order Cyclophyllidea (*Taenia solium*).

Anatomy. The scolex of a tapeworm serves primarily as an organ of attachment, though it also contains what little brain a tapeworm has. Considering the entire subclass Cestoda, the variety of holdfast organs developed by the scolex is remarkable (Fig. 87), consisting of groove-like, in-cupped, or ear-like suckers, and in addition, in some species, crowns of powerful hooks or rows of spines on a fleshy anterior protuberance called a rostellum, in some forms retractile into a pouch. In one order (Trypanorhyncha) there are long, protrusible, spiny proboscides retractile into canals in the neck (Fig. 87C). The scoleces of the tapeworms infesting mammals, however, are comparatively monotonous in form.

Like flukes, tapeworms are covered by a cuticle secreted by cells underlying it in the spongy mesodermal parenchyma in which all the

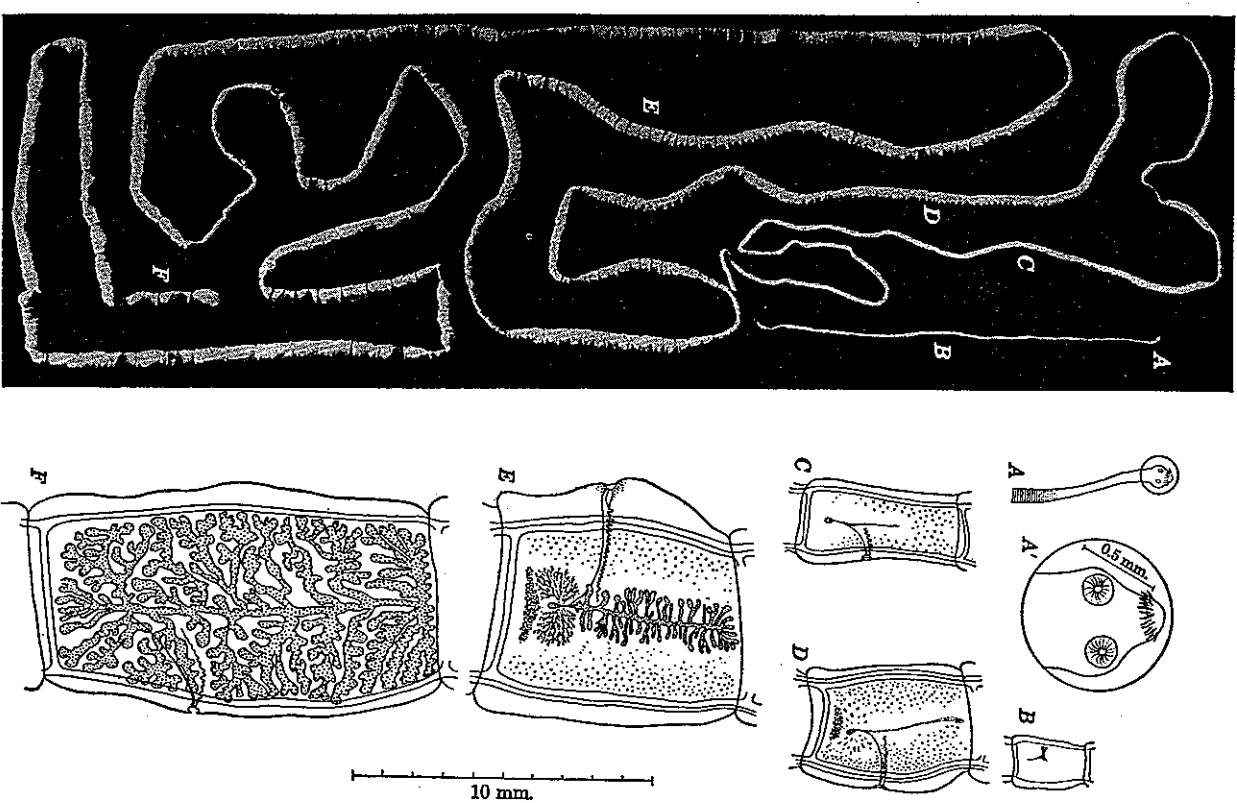


Fig. 86. *Taenia solium*, the pork tapeworm. Left, whole worm, about $\frac{1}{8}$ natural size. Right, enlarged parts of worms from regions indicated on whole worm, showing progressive development of proglottids. In C the testes are just beginning to appear; in D the male system is fully functional, but the female system is immature; in E both systems are fully mature and functional; and in F the ripe uterus has usurped the whole segment, only the vagina and sperm duct being still recognizable.

in a delicate hyaline sheath produced by the larva. The proboscis is fully formed but inverted, and the reproductive organs are sufficiently developed so that the sex is easily recognized. In *Moniliformis* larvae the hypodermis is expanded into broad flanges.

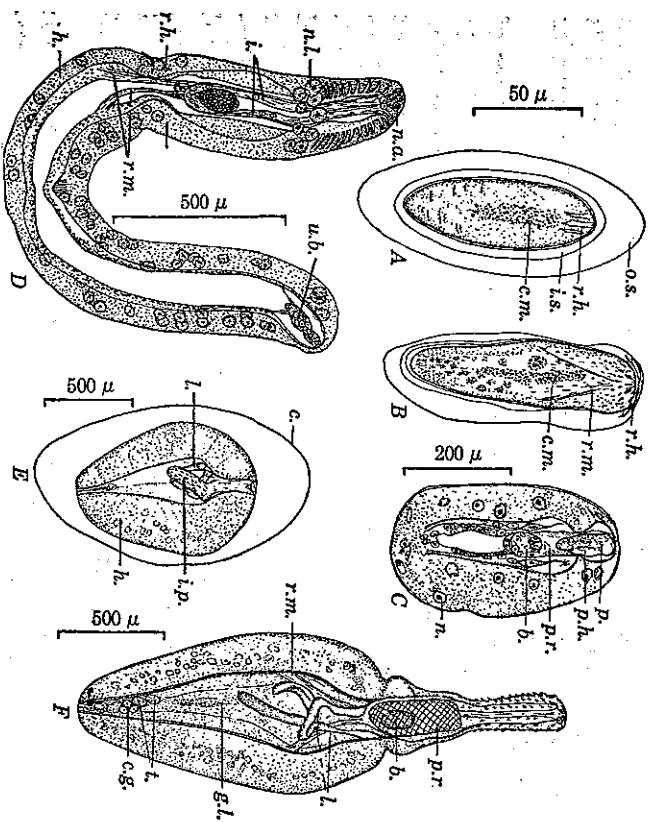


FIG. 111. Life cycle of *Moniliformis dubius*: A, egg; B, acanthor in process of escaping from egg shell and membranes; C, median sagittal section of larva from body cavity of roach 29 days after infection; D, acanthella dissected from enveloping sheath, about 40 days after infection; E, cystacanth from body cavity of roach, with proboscis inverted, about 50 days after infection; F, cystacanth freed from cyst and proboscis evaginated. Abbreviations: b, brain; c.g., cement glands; c.m., central nuclear mass; g.l., genital ligament; h., hypodermis; i., inveter muscles; i.p., inverted proboscis; i.s., inner shell; l., lemnisci; n., subcuticular nucleus; n.l., nuclei of apical ring; n.l., nuclei of lemniscal ring; o.s., outer shell; p., proboscis; p.h., developing proboscis hooks; p.r., proboscis receptacle; r.h., rostellar hooks; r.m., retractor muscle; t., testes; u.b., uterine bell. (After Moore, *J. Parasitol.*, 1946.)

Effects on Host. Acanthocephala damage their hosts principally by local injury and inflammation at the point of attachment of the spiny proboscis. When the worm moves and reattaches, the old sore may become infected by bacteria. Occasionally the worms cause perforation of the gut wall and precipitate a fatal peritonitis. In heavy infections, loss of appetite and interference with digestion may lead to unfitness. Dogs and coyotes infected with *Oncicola* (see p. 381) are said sometimes to develop rabies-like symptoms, suggesting the

possibility of transmission of a virus by the worms. Grassi and Calandruccio in 1888 reported acute pain and violent ringing in the ears experienced by the junior author 19 days after infecting himself with *Moniliformis* larvae.

Burlingame and Chandler (1941) showed that, as with some adult tapeworms, no true immunity to Acanthocephala is developed, resistance to reinfection being primarily a matter of competition for food and for favorable locations in the intestine.

Classification. The Acanthocephala constitute a small group of about a dozen families and about sixty genera which are quite widely divergent from other groups of worms but which are remarkably uniform among themselves, both in morphology and life cycle. Once placed in a single genus, *Echinorhynchus*, they were later (1892) divided into several families, then (1931) into two orders, which were expanded to three in 1936 and finally elevated by Van Cleave (1948) into a phylum containing two classes and four orders: class Metacanthocephala with the orders Palaeacanthocephala and Archiacanthocephala, and the class Eoacanthocephala with the orders Gyraacanthocephala and Neocanthocephala.

To the writer the characters used by Van Cleave for differentiating these groups seem trivial. For example, in the table of characters given for distinguishing the orders, the only one in which the Gyraacanthocephala and Neocanthocephala differ is the presence or absence of trunk spines, and even this character is variable in one of the other orders. No good character is presented for differentiating the two classes. For the present, therefore, we prefer to consider the Acanthocephala as constituting a single class with three orders, as proposed by Van Cleave in 1936, though we consider even this rather extreme.

1. **Palaeacanthocephala.** Proboscis hooks usually in long rows; spines present on trunk; nuclei in hypodermis usually fragmented; chief lacunar vessels in hypodermis lateral; single ligament sac in ♀ often breaks down; separate cement glands; eggs spindle-shaped, thin-shelled; mostly in fishes and aquatic birds and mammals, cystacanth in Crustacea.

2. **Eoacanthocephala.** Proboscis hooks usually in a few circles; trunk spines present or absent; nuclei in hypodermis few and large; chief lacunar vessels dorsal and ventral; distinct dorsal and ventral ligament sacs in ♀; syncytial cement glands; eggs ellipsoidal, thin-shelled; parasitic in fishes, except one in turtles, cystacanth in Crustacea.

3. **Archiacanthocephala.** Proboscis hooks either in long rows (e.g., *Moniliformis*) or in a few circles (e.g., *Oncicola* and *Maeracanthorhynchus*); no spines on trunk; nuclei in hypodermis few and large; chief lacunar vessels dorsal and ventral; dorsal and ventral ligament sacs persist in ♀; separate cement glands; eggs usually oval, thick-shelled; protonephridia present in some; parasitic in terrestrial vertebrates, cystacanth in grubs, roaches, etc.

Holmes (1973) Intestinal parasites

using rat intestine : position in gut is niche axis.

--- Acanthocephalan
(spiny-headed worm)
— Tapeworm

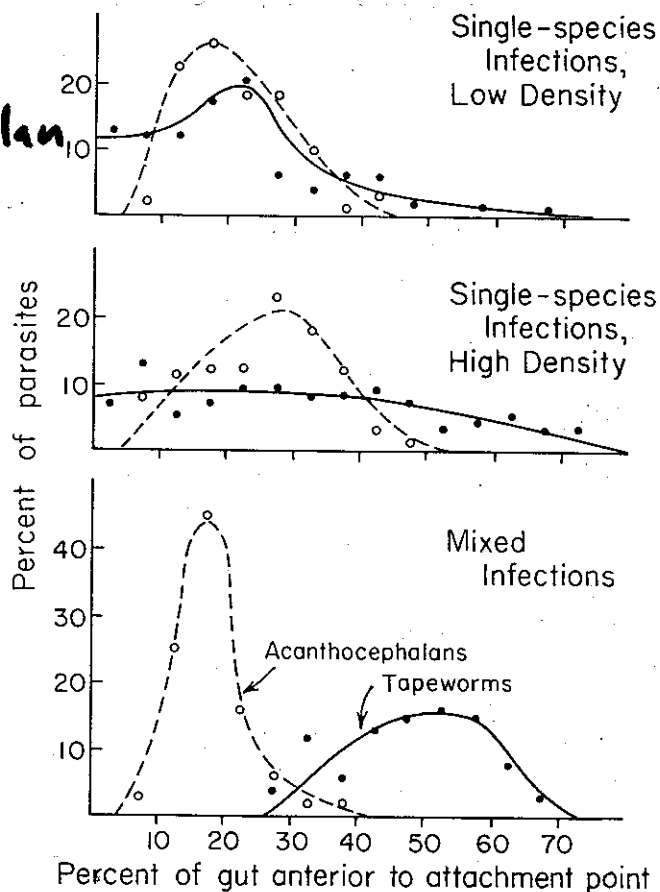


Figure 1 Effects of single-species and mixed infections on the intrainestinal distribution of the tapeworm *Hymenolepis diminuta* and the acanthocephalan *Moniliformis dubius*. Tapeworms are represented by solid dots and lines, and acanthocephalans by open dots and broken lines. The data points are from Holmes (84). The curves were drawn by eye.

Werner (1983) Bluegill - food type
predator avoidance

Interaction between two niche axes for
3 size classes.

December 1983

PREDATION RISK AND H.

TABLE 1. Average percent composition (± 1 SE) of the diet by habitat for the three bluegill size-classes (6 August-6 September). Row sums do not add to 100% because a small fraction ($\leq 3\%$) of prey could not be assigned to a specific habitat (see text for details).

		Vegetation	Plankton	Benthos
No predator	Small	9 \pm 2	19 \pm 5	69 \pm 7
	Medium	14 \pm 4	2 \pm 0.5	81 \pm 4
	Large	11 \pm 3	trace	86 \pm 3
Predator	Small	34 \pm 10	17 \pm 5	46 \pm 9
	Medium	9 \pm 3	16 \pm 6	74 \pm 7
	Large	14 \pm 5	6 \pm 4	78 \pm 6

Note shift

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TABLE 2. Mean individual dry mass (g) ± 1 SE for the three bluegill size-classes in the presence and absence of the predator. Final values are for the entire population recovered in the fall. Differences between means between predator and no predator treatments were determined by *t* test.

	Size-class					
	Small		Medium		Large	
	Predator	No predator	Predator	No predator	Predator	No predator
Initial mass (g)	0.28 \pm 0.01 (n = 44)		1.35 \pm 0.03 (n = 27)		3.64 \pm 0.12 (n = 30)	
Final mass (g)	0.90 \pm 0.02 (n = 348)	1.13 \pm 0.02*** (n = 359)	4.45 \pm 0.05 (n = 270)	4.35 \pm 0.05 (n = 270)	9.17 \pm 0.15 (n = 89)	8.64 \pm 0.15** (n = 81)
Increment (g)	0.62	0.85	3.10	3.00	5.53	5.00
Population increment (g)	191.0	269.5	768.8	750.0	392.6	230.0
Difference in population increment (g)	-78.5		18.8		72.6	

** *P* < .01.

*** *P* < .005.

Effects on growth rate of different
size classes with/without predator.

(1996)
DAYAN: Character displacement in Carnivore Guilds.

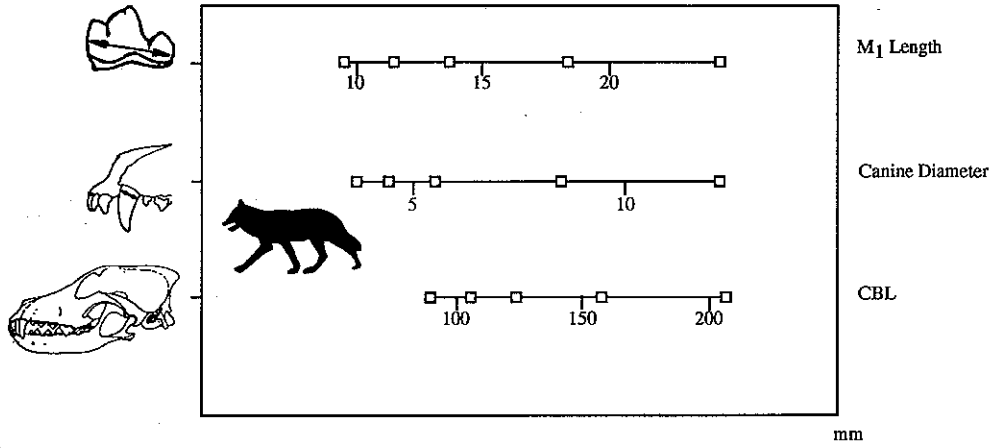


Figure 7.3. Lower carnassial lengths, canine diameters, and condylobasal skull lengths in the canid guild of Israel.

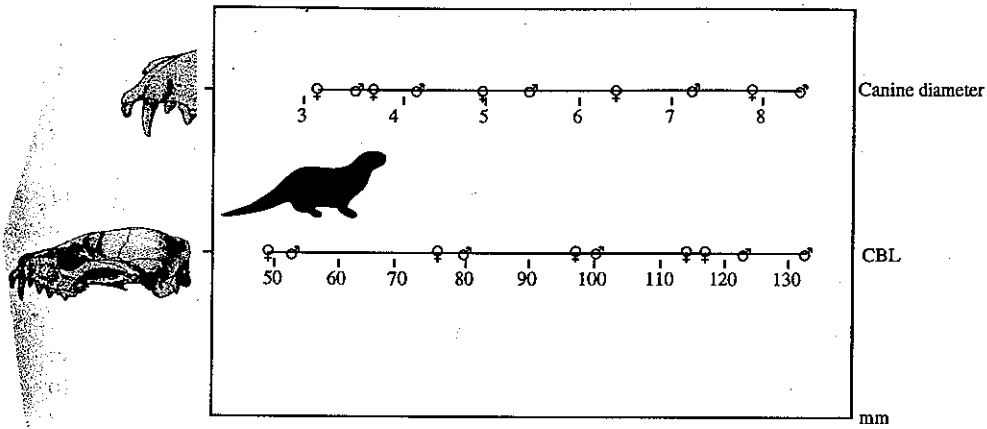


Figure 7.1. Canine diameters and condylobasal skull lengths of species in the mustelid/viverrid guild of Israel.

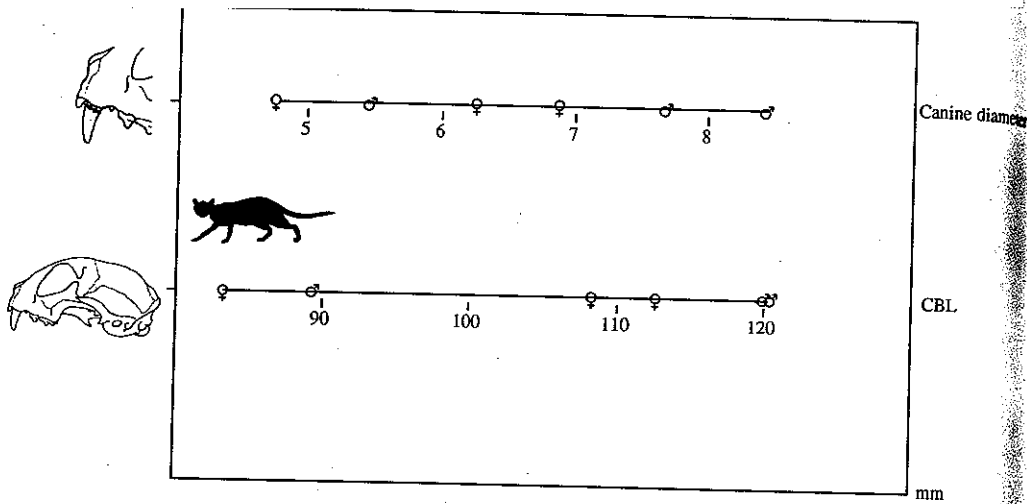


Figure 7.2. Canine diameters and condylobasal skull lengths of species in the small-felid guild of Israel.

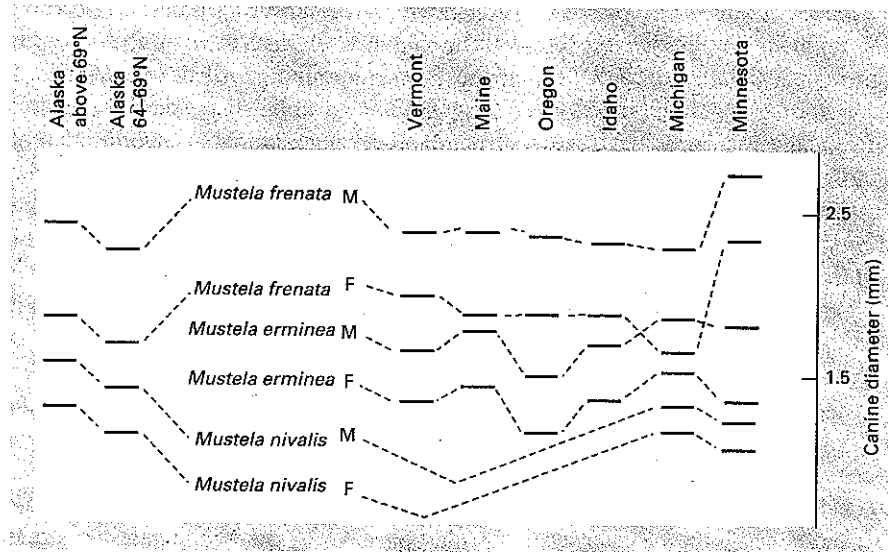


Figure 20.4 The mean diameters of the upper canines at eight locations in North America for each sex of three species of *Mustela* are shown as solid bars. For visual convenience dashed lines connect each sex of each species and the Alaskan populations are shown to the left. Despite considerable variation in number and identity of coexisting species, the spacing of canine sizes is remarkably even. (After Dayan *et al.*, 1989; Pimm & Gittleman, 1990.)

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DAYAN,
Carnivores.

Geographic shifts in niche: stronger support for character displacement.

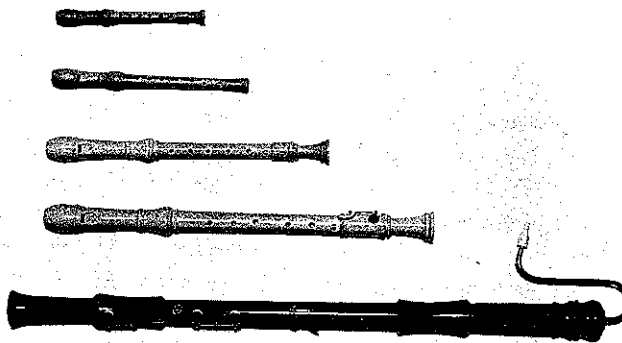


Figure 20.9 The conventional musical ensemble of recorders, which appears to conform to Hutchinson's size-ratio rule. (After Horn & May, 1977.) (Instruments kindly lent by R. Acott, Oxford. Photograph courtesy of B. Roberts.)

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Hairston (1980) Plethodon salamanders

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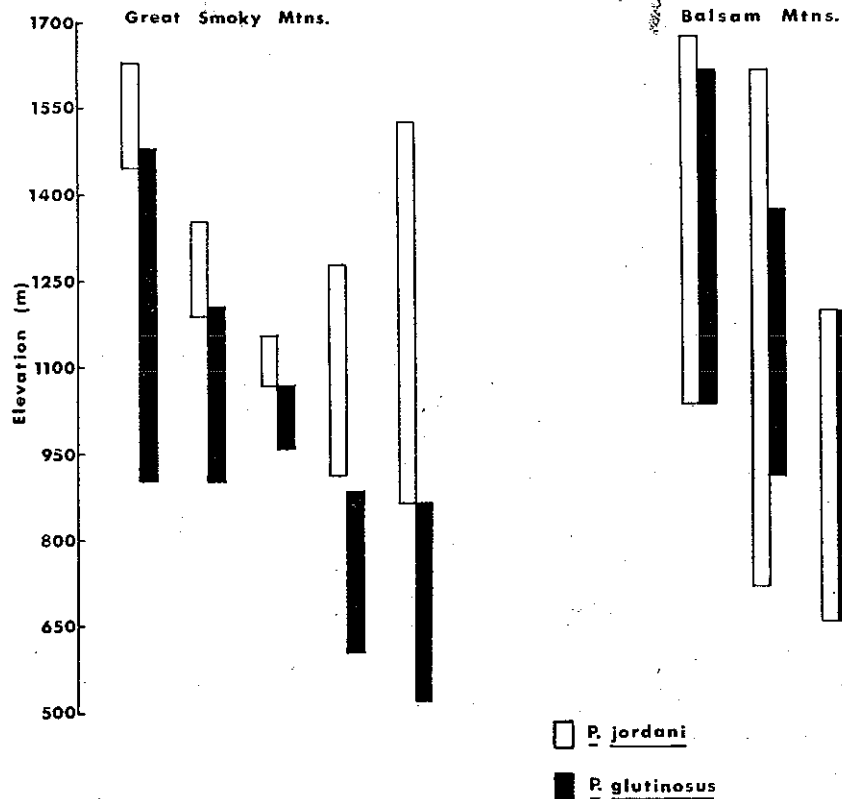


FIG. 1. The altitudinal distribution of *Plethodon jordani* and *P. glutinosus* in five vertical transects in the Great Smoky Mountains of North Carolina and Tennessee, and in three vertical transects in the Balsam Mountains of North Carolina.

Interspecific competition's effect
on altitudinal distribution

niche compression = competitive exclusion